

Spatial distribution, density, and habitat associations of queen conch *Strombus gigas* in St. Croix, US Virgin Islands

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ABSTRACT: Conventional stock assessment methods have been ineffective for determining the status of queen conch throughout the Caribbean, mainly due to a lack of available fishery-independent data. We examined queen conch populations on the northeastern coast of St. Croix, US Virgin Islands, using a 10 m radial survey sampling technique with sample sites stratified by water depth, habitat type, and management regime, encompassing both open and closed fishing areas. We completed 503 radial surveys and located 4773 queen conch, representing an overall density of 302 conch ha⁻¹. Densities of juvenile and adult queen conch were higher within Buck Island Reef National Monument (BIRNM) boundaries compared to open fishing areas. Densities of juvenile and adult queen conch were highest in habitats characterized as 50–90 and 10–50 % patchy seagrass, respectively. Shell length data suggest that the seagrass beds south of Buck Island are functioning as valuable nursery habitat for juvenile conch, and the presence of multiple juvenile cohorts indicates that larval recruitment in the area has been successful in recent years. Comparisons of data from this and previous studies indicate that the queen conch population in St. Croix is potentially stable under the current management approach and that BIRNM is providing the spatial protection required for the population to continue to recover. Given the spatial and temporal patchiness of queen conch distributions, standardized fishery-independent monitoring surveys should be repeated regularly to provide data sufficient to assess stock conditions and the efficacy of management measures.

KEY WORDS: Queen conch · Habitat use · Population structure · Marine protected area · Radial survey · St. Croix · US Virgin Islands

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INTRODUCTION

The queen conch *Strombus* (= *Lobatus*) *gigas* is an economically and culturally valuable mollusk throughout its tropical western Atlantic geographic range. It has been actively fished since the first inhabitants settled in the Caribbean islands centuries ago (Schapira et al. 2009). Reported landings of all strombid conch in the region peaked in the mid-1990s (FAO 2016) at an estimated annual wholesale value of USD 60 million (Chakalall & Cochrane 1997). In spite of localized stock depletions and pop-

ulation changes, queen conch still represent a significant commercial fishery in the Caribbean, partly due to increased international demand (Chakalall & Cochrane 1997). In response to the continued exploitation and potential collapse of the fishery, the queen conch was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora in 1992, regulating international trade of the species. Following the listing, landings abruptly peaked in 1994 and progressively declined over the next decade. Reported landings of strombid conch increased between 2007

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and 2013 and are again approaching peak levels (FAO 2016), although apparent increases may be the result of improved regional reporting, increased fishing and marketing of illegal or undersized conch, and exploitation of previously inaccessible populations (Theile 2005).

Fishing pressure in the northern US Virgin Islands, coupled with negative environmental impacts such as habitat degradation (Friedlander et al. 1994), severely reduced the local population and led to a complete closure of the fishery from 1988 to 1992. The fishery reopened in 1992 before formal management measures were officially adopted in 1994, and overfishing again rapidly depleted the population (Garcia-Moliner 1997). During the 5 yr moratorium, the fishery in St. Croix remained open, as territorial regulations already included a closed season, size limits, recreational fishing limits, and restricted sale of undersized individuals (Friedlander 1997). Territorial and federal management measures are now consistent across the US Virgin Islands and include size restrictions, seasonal closures during the peak spawning period from June 1 to October 31, and commercial and recreational bag limits. To understand the effects of management measures on animal populations, however, monitoring activities must provide sufficient data for conducting reliable stock assessments.

Fishery-dependent data, consisting of reported landings and measures of effort, are presently insufficient for understanding the status of queen conch populations in the region. Past attempts at completing stock assessments for queen conch in the US Caribbean were unsuccessful due to data deficiencies including a lack of recreational catch statistics, uncertainty in commercial catch statistics, inadequate fishery-independent data, and insufficient biological data (i.e. growth, mortality, reproduction, and age composition) (SEDAR 2007). Stock assessment models should include information from commercial and research surveys (Pennington & Stromme 1998), as inclusion of fishery-independent survey data in stock assessments can improve estimation of model parameters (Chen et al. 2003). Fishery-independent surveys are also increasingly important for enhancing scientific assessments when management regulations have modified fishing practices, such that landings do not reflect conditions of the stock (Rotherham et al. 2007).

Fishery-independent field surveys of queen conch are increasing in geographic range across the wider Caribbean. Population information from such surveys is typically presented as mean density per area

for each stratum sampled; however, these numbers are highly variable and fluctuate widely by locality, survey method, time of year, habitat type, and management strategy. Some of the highest overall densities reported from recent surveys were 247–1767 conch ha^{-1} from a protected park in Cuba (Cala de la Hera et al. 2012, Cala et al. 2013), 677 conch ha^{-1} from both fished and protected areas in the Turks and Caicos (Tewfik & Béné 2000), and 963 conch ha^{-1} from both fished and protected areas in Belize (Chan et al. 2013). Conversely, densities from other surveys were remarkably low. Mateo et al. (1998) reported mean densities within varied habitats in fished areas of Puerto Rico of 7.5 and 8.5 conch ha^{-1} on the east and west coasts, respectively. Stoner et al. (2012a) reported densities of adult conch in the Bahamas ranging from 1.3 to 144.5 conch ha^{-1} . Moreover, density estimates must be understood relative to the perceived age of the individual and environmental variables such as habitat type, area, season, or water depth to determine which factors may be influencing distribution patterns (Mateo et al. 1998, Posada et al. 1999, Gómez-Campo et al. 2010).

Since distributions of queen conch populations can vary both seasonally and annually, an ideal sampling design should incorporate repeated surveys at least every few years. However, temporal replication is difficult, and few studies have been successful in revisiting historical survey areas. Stoner et al. (2012a,b) repeated their surveys in the Bahamas in 1991, 1994, and 2011 and documented significant declines in conch densities over that time period. Queen conch population surveys in the US Virgin Islands have possibly the longest published record. The original surveys were completed in 1981 (Wood & Olsen 1983), and repeat surveys were conducted on several occasions over the next 30 yr (Boulon 1987, Friedlander et al. 1994, Friedlander 1997, Gordon 2002, 2010, Tobias 2005). The latter reports comprise ongoing survey efforts under the Southeast Area Monitoring and Assessment Program-Caribbean (SEAMAP-C), which show a decrease in mean conch density until 2001, followed by an increase through 2010 to the highest reported levels since 1981 (Gordon 2010).

The purpose of our study was to conduct surveys of queen conch on the northeastern shelf of St. Croix to (1) generate habitat-based fishery-independent density estimates suitable for contributing to stock assessment models, (2) quantify length-based differences (juvenile and adult age classes) in queen conch densities and distribution by management regime (i.e. inside and outside marine protected areas), and

(3) compare population density patterns with historical SEAMAP-C surveys conducted in the area.

MATERIALS AND METHODS

Our study area was on the northeastern coast of St. Croix, US Virgin Islands, and included a wide variety of reef-associated habitat types and 2 management areas (Fig. 1). A portion of Buck Island Reef National Monument (BIRNM) is located within the study area along with the St. Croix East End Marine Park (EEMP). BIRNM, originally established in 1961 and expanded to its current configuration in 2001, encompasses 7695 ha of land and underwater habi-

tat. Nearly half of the original national monument was designated as a no-take reserve, and the full extent of BIRNM has been closed to all extractive fishing since the expansion in 2001. According to the most recent benthic habitat maps, the northern section of BIRNM is dominated by colonized pavement, colonized pavement with channels, aggregate patch reef, and scattered coral-rock; the southern portion is mainly sand, continuous seagrass, and patchy seagrass beds of varying densities (Kendall et al. 2001). EEMP was established in 2003 and surrounds the eastern end of St. Croix from shore to 3 nautical miles. EEMP is a multiple-use park comprised of 4 management zones including recreation, wildlife preserve, no-take, and open fishing areas. The rules

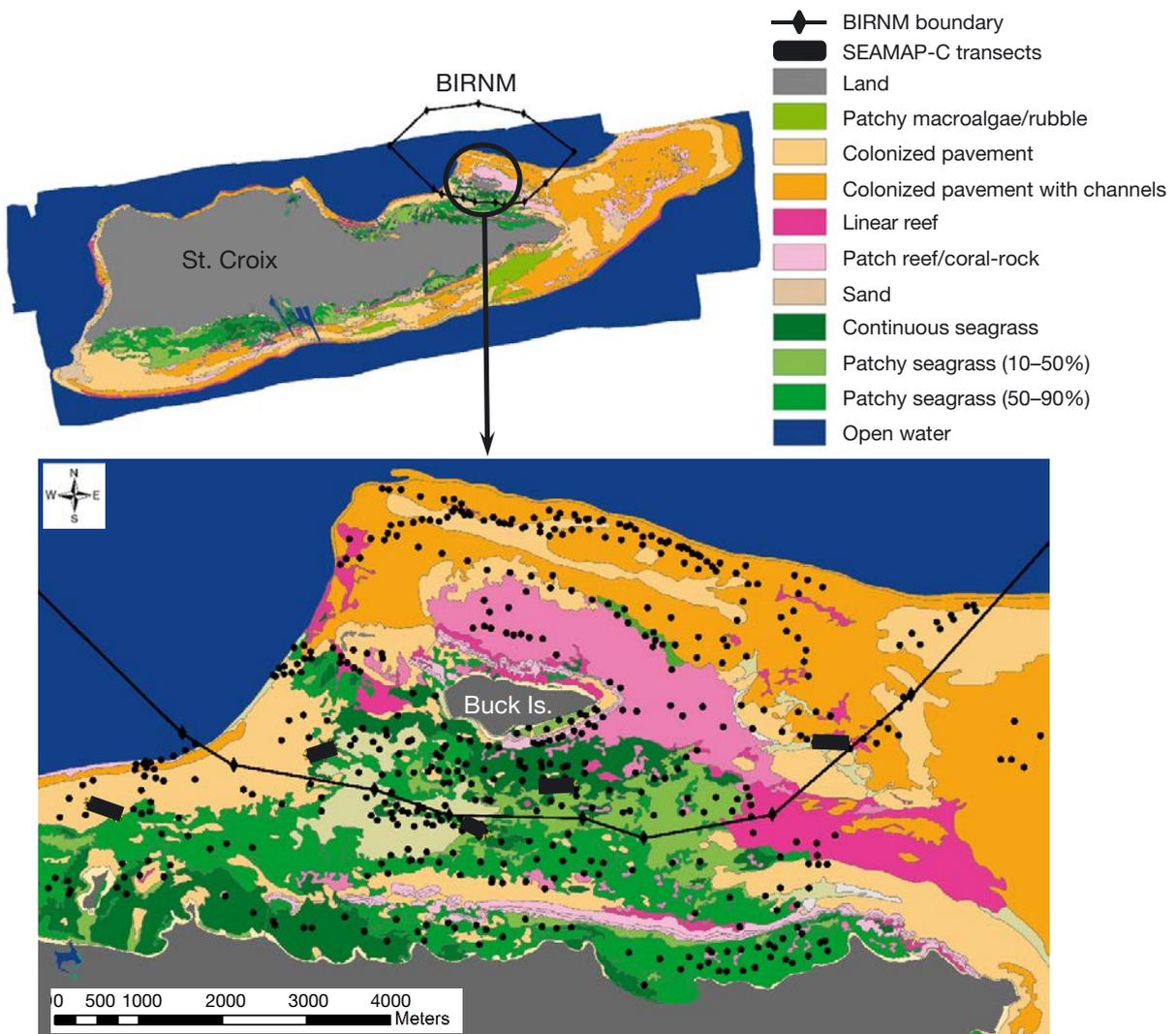


Fig. 1. St. Croix, US Virgin Islands, showing the spatial coverage and arrangement of benthic habitat types, the administrative boundary of Buck Island Reef National Monument (BIRNM, thin black line), our radial survey locations (black circles), and the 5 Southeast Area Monitoring and Assessment Program-Caribbean (SEAMAP-C) linear transects located within our study area (thick black lines). Transects are ordered numerically from west to east beginning with transect 1 on the left side of the map

and regulations governing the use of the zones were formally approved in 2007; however, boundary markers were not deployed until 2012, and the current regulations were not legally enforceable until then (Quinn 2008). Consequently, we considered EEMP an open fishing area in our study.

We surveyed queen conch populations using a radial survey sampling technique on 4 sampling occasions (September 2010; June, July, and September 2011). Sample sites were randomly stratified by water depth, benthic habitat type, and management regime, ensuring that habitats and depth zones in open and closed fishing areas were adequately sampled. Additional sample sites were selected to coincide with the beginning, middle, and end of the 5 SEAMAP-C linear transects located within our study area to facilitate comparisons between survey methods (Fig. 1).

At each sample site, we dropped a weighted line attached to a buoy and recorded the location using a hand-held GPS receiver. Divers descended to the bottom, where they clipped a 10 m survey line above the weight and recorded water depth. The divers, stationed at the midpoint and end of the survey line, swam the free end of the line around the weighted

center point and searched the entire circular area (314 m²) for conch. Shell length (tip of the spire to the anterior end of the siphonal canal) of each queen conch was measured *in situ* with calipers and recorded. Shell lip thickness of queen conch with flared lips was also measured at the area of greatest thickness (i.e. approximately midway along the flared outer lip and 3 cm in from the edge of the shell). Observations of reproductive activity were recorded as either active mating, spawning, or the presence of egg masses on the substrate.

Maturity status was assigned to each conch based on the current fishing regulations in the US Virgin Islands: legal queen conch must be a minimum of 228.6 mm (9 inches) in shell length or have a minimum lip thickness of 9.5 mm (3/8 inch). For analytical purposes, conch with shell measurements larger than either of these values were classified as adults (i.e. legal); otherwise, they were classified as juveniles (i.e. undersized). We elected to separate the age classes using this method to eliminate the subjectivity in visually characterizing completeness of the flared lip, to reduce potential differences in age assessment between individual divers, and to facilitate interpretation of our results in a fishery context.

Table 1. Abundance and densities of queen conch *Strombus gigas* shown by habitat type and depth bin for the entire study area, Buck Island Reef National Monument (BIRNM), and the surrounding areas open to regulated fishing. Densities are means expressed as conch ha⁻¹ ± SE; the actual number of conch counted can be calculated by multiplying the mean density by the survey area (0.0314 ha) and the number of surveys

Habitat and depth	All areas				BIRNM			
	No. of surveys	Juveniles	Adults	Overall	No. of surveys	Juveniles	Adults	Overall
Habitat type								
Colonized pavement	115	34.3 ± 13.4	62.3 ± 16.1	96.6 ± 25.0	87	23.8 ± 11.8	58.5 ± 17.7	82.3 ± 23.9
Colonized pavement with channels	38	1.7 ± 1.2	9.2 ± 3.3	10.9 ± 3.6	37	1.7 ± 1.2	9.5 ± 3.4	11.2 ± 3.7
Linear reef	41	2.3 ± 1.3	13.2 ± 6.4	15.5 ± 6.6	34	1.9 ± 1.3	15.0 ± 7.6	16.9 ± 7.7
Patch reef/coral-rock	53	19.8 ± 5.5	81.1 ± 18.8	100.9 ± 20.7	43	23.7 ± 6.5	98.5 ± 22.4	122.1 ± 24.3
Patchy macroalgae/rubble	58	103.7 ± 44.2	103.7 ± 23.8	207.4 ± 54.6	27	50.7 ± 13.5	167.4 ± 45.8	218.1 ± 48.4
Sand	38	15.9 ± 4.8	77.9 ± 29.5	93.8 ± 31.5	21	19.7 ± 7.3	121.3 ± 51.1	141.0 ± 54.3
Patchy seagrass (10–50%)	50	610.5 ± 199.2	128.6 ± 27.3	739.1 ± 197.9	28	818.5 ± 341.1	188.7 ± 43.7	1007.2 ± 335.1
Patchy seagrass (50–90%)	66	878.2 ± 184.3	64.6 ± 11.5	942.9 ± 182.3	24	1452.3 ± 421.0	96.8 ± 25.2	1549.1 ± 411.9
Continuous seagrass	44	390.7 ± 92.2	55.7 ± 16.9	446.4 ± 94.9	6	1013.3 ± 417.9	265.3 ± 49.0	1278.5 ± 374.0
Depth bin (m)								
0–6	80	151.6 ± 34.6	18.7 ± 5.3	170.3 ± 36.0	26	67.3 ± 47.6	39.2 ± 14.3	106.5 ± 55.9
7–12	226	200.8 ± 37.3	63.8 ± 9.4	264.6 ± 39.6	136	103.0 ± 33.0	66.9 ± 12.8	169.9 ± 37.0
13–18	142	419.0 ± 108.0	81.8 ± 11.9	500.8 ± 107.7	105	503.2 ± 143.4	95.5 ± 15.6	598.7 ± 142.7
19–24	50	8.9 ± 3.3	117.1 ± 33.6	126.1 ± 34.4	36	7.1 ± 3.3	145.0 ± 44.7	152.1 ± 46.1
25–30	5	0	216.5 ± 126.8	216.5 ± 126.8	4	0	270.6 ± 146.5	270.6 ± 146.5
Overall	503	233.5 ± 35.7	68.5 ± 6.7	302.1 ± 36.4	307	224.3 ± 52.6	86.2 ± 9.9	310.4 ± 53.4

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At each sample site, benthic habitat type was visually characterized and assigned to a habitat type following published benthic habitat map categories (Kendall et al. 2001). To facilitate analysis, we combined the individual/aggregate patch reef and scattered coral-rock into one habitat category and the rubble and patchy macroalgae habitat types into another category because of their low sample counts and physical similarities (nearly all rubble sites were colonized by macroalgae). We also combined the 10–30 and 30–50% patchy seagrass into a 10–50% patchy seagrass category and the 50–70 and 70–90% patchy seagrass into a 50–90% patchy seagrass category to account for the subjectivity and individual variability in accurately assigning a survey site to one of these habitat types.

The data were not normally distributed and failed the test for homogeneity of variances, which is typical for these types of population surveys with large variances and many zeros. Attempts to transform the data did not improve the results of these tests, so non-parametric methods were employed for data analyses. Means and standard errors were calculated from raw count data. We used Kruskal-Wallis tests to examine differences in density estimates by habitat type and depth zone, followed by post hoc multiple comparison testing with Bonferroni corrections to identify the significance levels associated with each comparison between variables. We used Mann-

Whitney U tests to examine differences in density estimates between management zones. Kolmogorov-Smirnov (K-S) tests were used to examine potential differences in shell length and lip thickness frequency distribution patterns. A significance level of $\alpha = 0.05$ was used for the interpretation of test results. Statistical analyses were conducted using Statistica (version 11).

RESULTS

We conducted 503 radial surveys (Fig. 1) and located and measured 4773 queen conch, 3690 juveniles and 1083 adults (Table 1). Conch were present in every habitat type and depth zone surveyed, except for colonized pavement with channels in the 25–30 m depth zone within the open fishing area. The mean density across the entire study area was 302.1 conch ha^{-1} . Juvenile conch had an overall mean density of 233.5 ha^{-1} , while the overall mean density of adults was much lower at 68.5 conch ha^{-1} (Table 1). Overall densities of conch were significantly higher inside BIRNM than in the open fishing areas (Mann-Whitney U test, $U = 26\,630.5$, $p = 0.0237$), as were adult densities ($U = 26\,661.5$, $p = 0.0176$). Juvenile densities were statistically higher in the open fishing areas ($U = 23\,266.0$, $p < 0.0001$), although the mean value was only slightly higher (Table 1).

We surveyed nearly 16 ha across 9 benthic habitat types including colonized pavement, patch reef/scattered coral-rock, linear reef, sand, macroalgae, and seagrass beds of varying shoot densities. Queen conch densities were significantly different across habitat types (Kruskal-Wallis test, $H = 175.6$, $p < 0.0001$) with all depths combined (Table 1). The highest mean density occurred in 50–90% patchy seagrass at 942.9 conch ha^{-1} , and the lowest mean density was in colonized pavement with channels at 10.9 conch ha^{-1} across all water depths (Table 1), with significant differences between the vegetated (i.e. various seagrass densities) habitats and the nonvegetated/hard-bottom habitats for both juveniles and adults. Juvenile conch density was highest in 50–90% patchy seagrass, while the lowest densities were in colonized pavement with channels and linear reef (Table 1). The density of adult conch was highest in 10–50% patchy seagrass at 128.6 conch ha^{-1} and lowest in colonized pavement with channels at 9.2 conch ha^{-1} (Table 1).

We grouped water depth into 5 bins to maintain consistency and facilitate comparisons with the SEAMAP-C density data. Overall, the mean density of queen conch increased with depth to a maximum

No. of surveys	Open fishing areas		Overall
	Juveniles	Adults	
28	67.1 ± 40.2	73.9 ± 36.7	141.0 ± 70.4
1	0	0	0
7	4.5 ± 4.2	4.5 ± 4.2	9.1 ± 8.4
10	3.2 ± 3.0	6.4 ± 4.0	9.5 ± 4.6
31	149.9 ± 81.0	48.3 ± 13.5	198.2 ± 93.0
17	11.2 ± 5.9	24.3 ± 8.6	35.6 ± 10.2
22	345.8 ± 104.1	52.1 ± 16.7	397.9 ± 104.9
42	550.2 ± 137.6	46.2 ± 9.7	596.5 ± 137.2
38	292.3 ± 71.9	22.6 ± 10.5	315.0 ± 72.5
54	192.2 ± 44.8	8.8 ± 3.1	201.0 ± 45.4
90	348.7 ± 76.6	59.1 ± 13.4	407.8 ± 79.9
37	179.8 ± 63.9	43.0 ± 8.3	222.8 ± 62.9
14	13.6 ± 7.7	45.5 ± 25.5	59.1 ± 24.9
1	0	0	0
196	248.0 ± 39.9	40.9 ± 6.8	288.9 ± 41.4

value of 500.8 conch ha⁻¹ in 13–18 m. Densities decreased sharply at depths greater than 18 m, and the differences were significant ($H = 14.3$, $p = 0.0063$). This pattern was driven by the abundance of juvenile conch, which had a maximum density in 13–18 m and were absent in the 25–30 m depth bin (Table 1). The differences between densities of juvenile conch by depth bin were significant ($H = 26.9$, $p < 0.0001$), and the 19–24 m bin had significantly lower juvenile densities than each of the shallower bins (0–6 m, $p = 0.0013$; 7–12 m, $p = 0.0320$; and 13–18 m, $p = 0.0008$). Juvenile conch densities were higher in the open areas than in BIRNM across all depth bins except 13–18 m (Table 1). Densities of adult conch also increased with depth from a minimum of 18.7 conch ha⁻¹ in 0–6 m to a maximum mean density of 216.5 conch ha⁻¹ in 25–30 m (Table 1), and these differences were significant ($H = 30.8$, $p < 0.0001$). The significant differences in adult densities occurred between the 0–6 m bin and all other depth bins, with the exception of the deepest bin (7–12 m, $p = 0.0436$; 13–18 m, $p < 0.0001$; 19–24 m, $p = 0.0157$; 25–30 m, $p = 0.3602$).

Shell lengths of juvenile conch ranged from 3.0 to 22.9 cm in BIRNM and from 7.0 to 22.9 cm in the open zones. As noted previously, a total shell length of 22.9 cm or a lip thickness of 9.5 mm was the threshold size by which conch were classified as either juveniles or adults. The length frequency of juveniles in BIRNM had a bimodal distribution dominated by conch of 7–9 cm (≤ 1 yr old), with a minor peak at 19–21 cm (Fig. 2). The distribution for juveniles in the open areas had 3 peaks at 9–10, 13–15, and 18–20 cm, and the frequency distributions were significantly different between management zones (K-S test, $p < 0.0001$). The length frequency distribution of adults was also significantly different between BIRNM and the open fishing areas (K-S test, $p = 0.0232$); higher overall abundance and larger shell lengths occurred within the protected waters of BIRNM (Fig. 2). Shell lengths of adult conch ranged from 13 to 29 cm in BIRNM and from 15 to 30 cm in the open fishing zones. Adult shell lengths in both zones were normally distributed, peaking at 20–22 cm in BIRNM and at 20–24 cm in the open fishing areas (Fig. 2).

Shell lip thickness varied spatially between the 2 management zones (Fig. 3). There was a significant difference in the frequency distribution of shell lip thickness between adult conch in BIRNM and those in the open fishing areas (K-S test, $p < 0.0001$). The overall range of lip thicknesses was similar (0.2–3.2 cm in BIRNM and 0.2–3.0 cm in open fishing

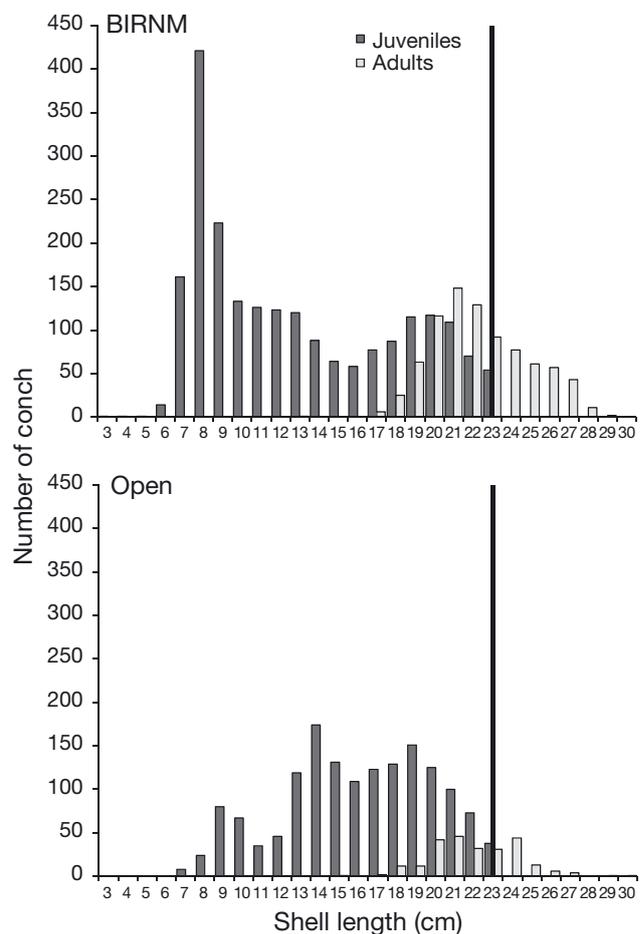


Fig. 2. Shell length frequency distributions for juvenile and adult queen conch inside Buck Island Reef National Monument (BIRNM, top) and the surrounding open fishing areas (bottom). The black vertical line indicates the (legal) shell length division between juvenile and adult age classes. Adult conch located to the left of each black vertical line (i.e. < 23 cm shell length) were designated as adults since their lip thicknesses were greater than 9.5 mm. See 'Materials and methods' for a complete description of age class categories

areas), but adult queen conch in the open fishing areas had slightly thinner lips ($\bar{x} = 1.4$ cm, $SE = 0.04$) than those inside BIRNM ($\bar{x} = 1.6$ cm, $SE = 0.02$).

The length frequency distributions of queen conch differed as shell length increased across almost all habitat categories in both BIRNM and open zones, and the overall distribution was governed by the abundance of juvenile conch. The percentage of the population in most of the vegetated habitats (continuous and 10–50% patchy seagrass) in BIRNM decreased as shell length increased (Fig. 4) but increased in the hard-bottom and reef habitats (colonized pavement, colonized pavement with channels, linear reef, patchy macroalgae/rubble, and aggregate and individual patch reef/scattered coral-rock).

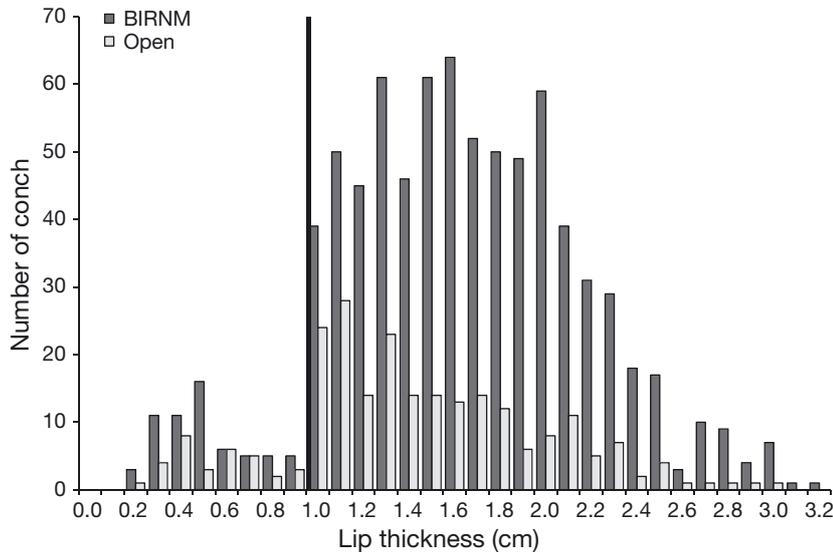


Fig. 3. Lip thickness frequency distribution for flared adult queen conch inside Buck Island Reef National Monument (BIRNM) and the surrounding open fishing areas. The black vertical line indicates the lip thickness (≥ 9.5 mm) at which flared queen conch can be legally harvested in the open fishing areas. Adult conch located to the left of the black vertical line were designated as adults since their shell lengths were greater than 23 cm. See 'Materials and methods' for a complete description of age class categories

In the open fishing areas, the percentage of the population in 10–50% patchy seagrass decreased with increasing shell length but remained about the same in 50–90% patchy seagrass. Large conch in the open fishing areas shared a similar pattern to those in BIRNM; the percentage of the population in hard-bottom and patchy macroalgae/rubble habitats increased with shell length. The percentage of juvenile queen conch was high in all soft-bottom habitats, and the percentage of juveniles in hard-bottom habitats increased with shell length (Fig. 5). The percentage of the adult queen conch population varied by habitat type, but overall the percentage of adults in soft-bottom habitats decreased with shell length (Fig. 5).

Overall shell length was significantly different among depth bins ($H = 796.6$, $p < 0.0001$), and the 2 shallow bins were different from the 3 deeper bins ($p < 0.0001$). In the shallowest depth bins, 0–6 and 7–12 m, the length frequency distributions were driven by queen conch in the open fishing areas (Fig. 6A), particularly juveniles (Fig. 6B). In the deeper depth bins (13–18, 19–24, and 25–30 m), the length frequency distributions were governed by the patterns within BIRNM (Fig. 6A), which were dominated by juveniles in the 13–18 m depth bin (Fig. 6B) and adults in the 2 deepest bins (Fig. 6C). Juvenile conch were uncommon in the 19–24 m bin, and only adults were located at depths of 25–30 m.

We observed reproductive activity either as copulation or active spawning (i.e. laying egg masses) associated with 26 flared adult conch. Of these flared adults, 18 individuals were spawning, 4 pairs were mating, and 1 conch was simultaneously mating and spawning. The mean shell length and lip thickness for adults involved in reproductive activity was 21.5 cm ($SE = 0.43$) and 1.6 cm ($SE = 0.08$), respectively. Nearly all reproductive behavior occurred in BIRNM in 13–18 m of water; only 1 conch was spawning in areas open to fishing. Spawning occurred in colonized pavement, colonized pavement with channels, patch reefs, patchy macroalgae, patchy seagrass, and sand. Mating was only recorded in 10–50 and 50–90% patchy seagrass habitats.

We compared our radial survey method with the SEAMAP-C linear transect method by sampling at the beginning, middle, and end point of the 5 SEAMAP-C linear transect locations within our study area during the September 2011 survey period. At SEAMAP-C transect sites 1 and 4, densities of conch were higher in our study, but at SEAMAP-C sites 2, 3, and 5, densities were lower in our study. The greatest difference occurred at transect 2, where we estimated a mean density of $79.6 \text{ conch ha}^{-1}$ compared to the reported SEAMAP-C density of $702.2 \text{ conch ha}^{-1}$ at that same location (Gordon 2010). Densities for both studies were highest at site 4, where SEAMAP-C reported a mean density of $956.6 \text{ conch ha}^{-1}$ (Gordon 2010) and we estimated a density of $1263.3 \text{ conch ha}^{-1}$.

Densities by major habitat category demonstrated similarities and differences between the 2 studies (Fig. 7). The highest overall and juvenile densities for both studies occurred in seagrass; however, we estimated the highest adult density in rubble ($\bar{x} = 236.5 \text{ ha}^{-1}$, $SE = 135.6$), while the highest SEAMAP-C adult density occurred in seagrass ($\bar{x} = 114.8 \text{ ha}^{-1}$, $SE = 68.6$). Both studies reported the lowest densities for all age classes of conch in coral habitat. The overall density of conch in coral reported by SEAMAP-C (Gordon 2010) was $14.6 \text{ conch ha}^{-1}$ ($SE = 9.2$), and in our study, we estimated a mean density of $63.7 \text{ conch ha}^{-1}$ ($SE = 12.8$). Densities grouped into depth bins indicated that juveniles increased with depth to

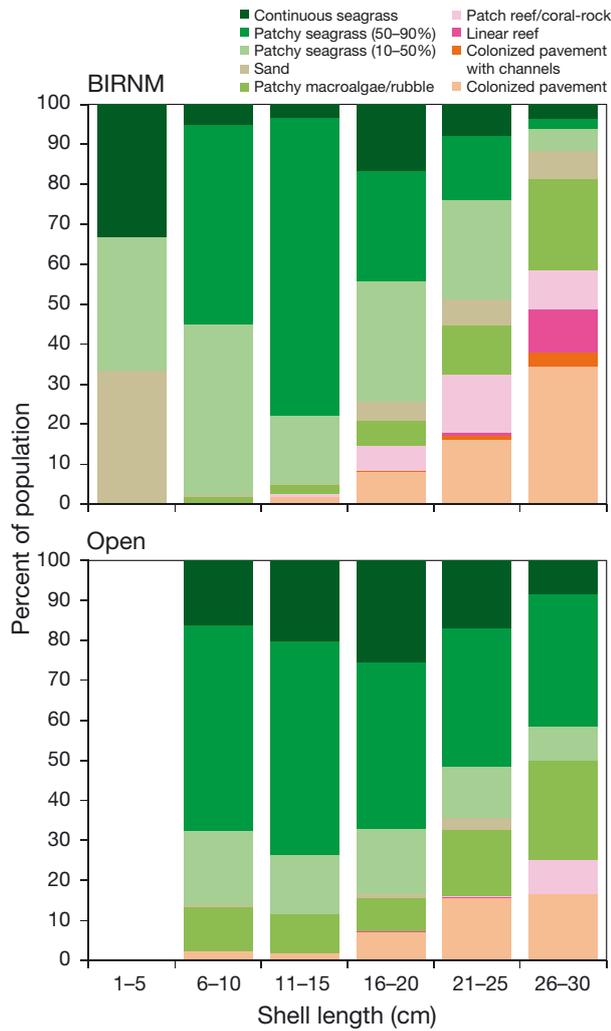


Fig. 4. Shell length distribution by habitat type of queen conch in Buck Island Reef National Monument (BIRNM, top) and the surrounding open fishing areas (bottom) expressed as a percent of the total population surveyed

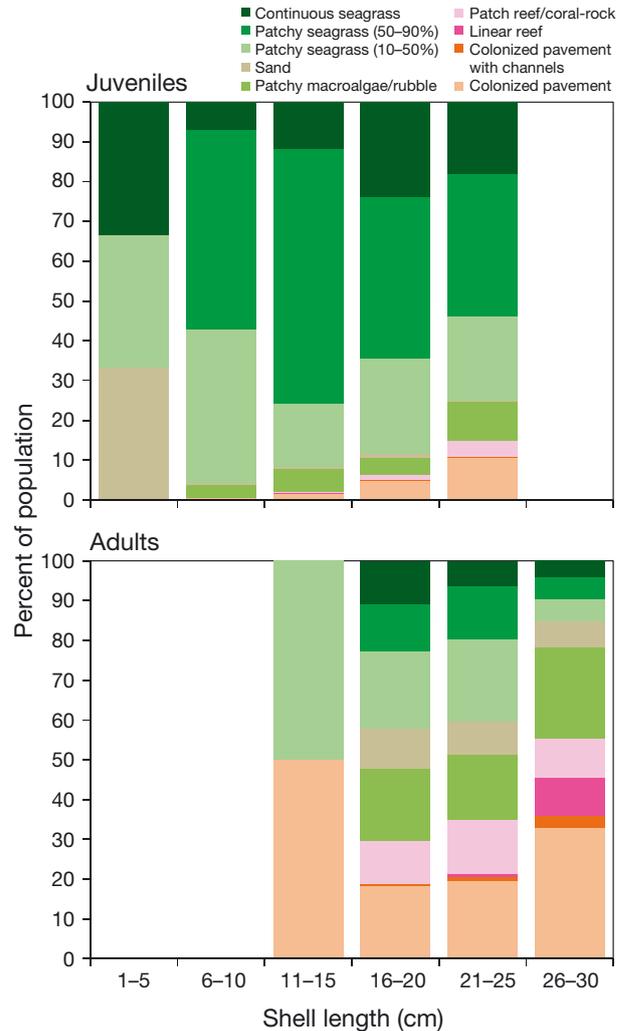


Fig. 5. Shell length distribution by habitat type of all juvenile (top) and adult queen conch (bottom) expressed as a percent of the total population surveyed

13–18 m in our study, compared with the SEAMAP-C study that reported lower but approximately equal densities between the 7–12 and 13–18 m depth bins during their surveys (Fig. 8). Densities of adults increased consistently with depth in our study, reaching a maximum of 216.5 adults ha⁻¹ in the 25–30 m depth bin. The SEAMAP-C surveys also demonstrated an increasing trend in adult densities with depth, although the increases between the depth bins were considerably lower than results from this study (Fig. 8).

DISCUSSION

Queen conch on the northeastern shelf of St. Croix had a patchy distribution, and the highest densities

occurred in seagrass habitats both inside and outside BIRNM boundaries. The high overall densities we reported were due to the abundance of young juveniles (7–9 cm) present in seagrass habitats in shallow water, particularly during the September 2011 surveys. Sparse to moderate seagrass is commonly reported as the dominant feature of queen conch nursery areas (Weil & Laughlin 1984, Stoner & Waite 1990, Sandt & Stoner 1993, Delgado et al. 1998, Stoner 2003), although water depth, tidal currents, and proximity to historical nursery grounds are also important characteristics (Stoner et al. 1996). The length frequency distribution and the high densities of small conch present in our surveys indicate that the seagrass beds located just south of Buck Island are functioning as nursery habitat for young juvenile queen conch.

Adult queen conch were more equitably distributed than juveniles among aggregate patch reef/coral-rock, patchy macroalgae/rubble, sand, and seagrass; however, there was a general trend toward

increasing abundance with shell length in hard-bottom habitats, particularly colonized pavement. Lip thickness of flared adults was also correlated with habitat type. In soft-bottom habitats, there was

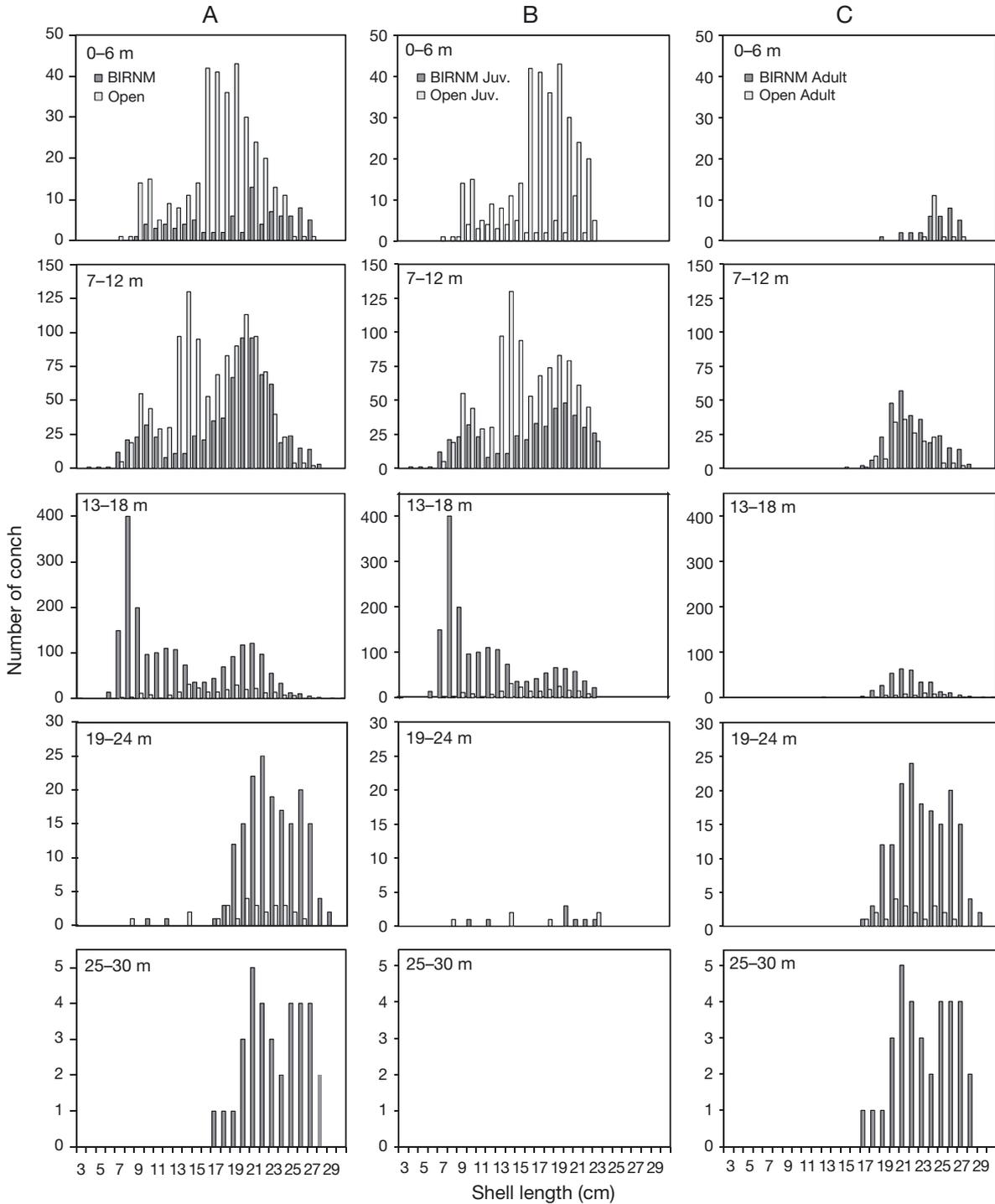


Fig. 6. Shell length frequency distributions by age class for (A) all juvenile and adult queen conch combined, (B) juvenile queen conch inside Buck Island Reef National Monument (BIRNM) and surrounding open fishing areas, and (C) adult queen conch inside BIRNM and surrounding open fishing areas in 6 m depth bins. No queen conch were present in the 25-30 m depth bin within the open fishing areas. Note the differences in the vertical scales

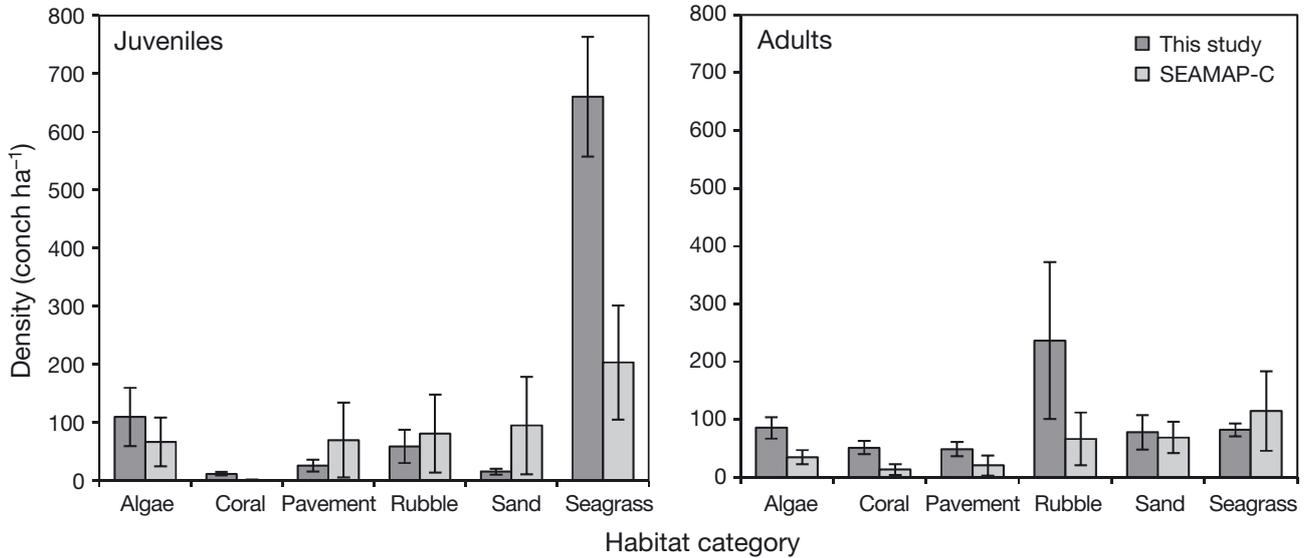


Fig. 7. Densities of juvenile and adult queen conch by condensed habitat category for this study and values calculated from data available in the Southeast Area Monitoring and Assessment Program-Caribbean (SEAMAP-C) report (Gordon 2010). Shown are mean densities \pm SE for the 6 major habitat types

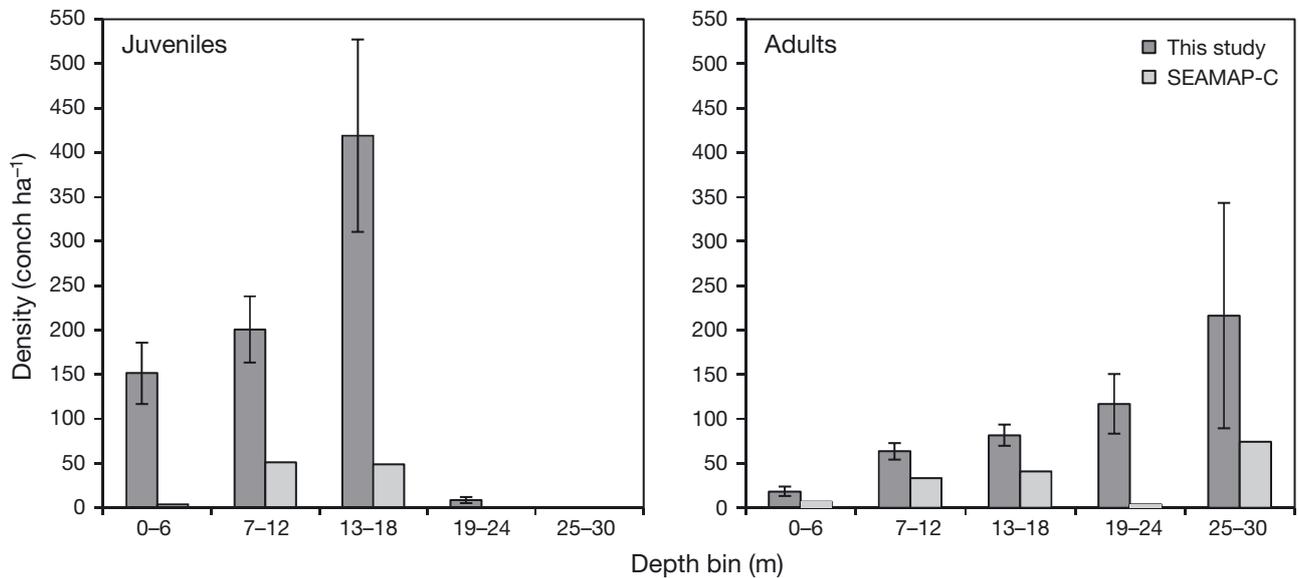


Fig. 8. Densities of juvenile and adult queen conch by depth bin for this study and values recalculated from data available in the Southeast Area Monitoring and Assessment Program-Caribbean (SEAMAP-C) report (Gordon 2010). Mean densities \pm SE (this study only) for the 6 depth bins are shown. It was not possible to calculate SE values from the available SEAMAP-C data

an overall trend of decreasing densities as lip thickness increased, but in hard-bottom habitats, adult densities increased with lip thickness. Similar to Valès & Oxenford (2012), the adult queen conch located on hard-bottom habitats within BIRNM had the largest shell lengths and the thickest lips of queen conch throughout the study area. These results suggest that BIRNM is providing favorable conditions for

growth and survival as well as long-term protective benefits for queen conch within its boundaries.

The interaction of environmental and biological variables (e.g. substrate type and quality, food supply, predation pressure) may influence distribution patterns, creating an appearance that queen conch are actively selecting for or avoiding particular habitat types, even though this may not be the case

(Glazer & Kidney 2004). In our study, adult queen conch were broadly associated with a variety of habitat types; therefore, depth may have exerted a stronger influence on our understanding of their spatial distribution patterns. The highest densities of adult conch occurred in deep water of 19–30 m, similar to other surveys where adult densities increased with water depth (Friedlander et al. 1994, Posada et al. 1999, Vallès & Oxenford 2012). Fishing pressure also can alter apparent distributions of mature conch in relation to water depth, and high densities of adult conch have been reported in shallow waters in unfished populations (Weil & Laughlin 1984, Stoner & Ray 1996, Glazer & Kidney 2004). The high density of adult conch in deep water within BIRNM, however, suggests that fishing activity was not the primary influence on their distribution pattern at this depth zone.

Distribution patterns of localized queen conch populations can result from density-dependent mechanisms. Glazer & Kidney (2004) postulated that high densities of queen conch coupled with limited availability of preferred habitats may pressure individuals in the population to move to less desirable habitats. However, this type of selection pressure was not evident in our study area since adults were less common in hard-bottom habitats such as colonized pavement with channels and linear reef. These 2 habitat categories alone comprised approximately 35% of the available habitat within BIRNM, but we located only 3% of adult conch in these habitat areas. Béné & Tewfik (2003) reported another potential density-dependent effect in the form of reduced growth rates in areas with high densities (301 conch ha⁻¹) of adult queen conch within an enclosed marine reserve in the Turks and Caicos Islands. Although the overall density of adult queen conch within BIRNM was substantially lower than that reported from the Turks and Caicos (Béné & Tewfik 2003), the numerous large and old individuals present within the population suggest that inhibition of overall growth is not occurring in the reserve.

Evaluating the effectiveness of size regulations on fished stocks can be difficult. Our use of the size limits established by territorial fishery regulations to classify adult (i.e. legal) and juvenile (i.e. undersized) individuals allows us to more directly assess density differences between fished and protected areas, assuming a reasonable level of compliance, rather than using an estimated biological measure of maturity. The onset of sexual maturity in queen conch varies geographically, and the division of individual conch into maturity categories based on visual as-

sessments of shell morphology is subjective. Shell length alone provides no real information about whether or not a queen conch is sexually mature (Stoner et al. 2012c), and even using lip thickness as an indicator of maturity is ambiguous. Historical studies report that some queen conch mature with relatively thin lips less than 7 mm (Egan 1985, Appeldoorn 1988a), whereas recent studies indicate that maturation occurs later, at larger sizes, and differs by gender. Avila-Poveda & Baqueiro-Cárdenas (2006) reported that 50% of female and male queen conch in Colombia reached maturity at a shell length of 249 and 234 mm and lip thicknesses of 17.5 and 13 mm, respectively. In the Bahamas, 50% of female and male queen conch reached maturity at smaller shell lengths but with thicker flared lips, measuring 206 and 210 mm in shell length and 26.2 and 24 mm in lip thickness, respectively (Stoner et al. 2012c). Both studies advocated for increases in the minimum shell lip thickness for legal harvest: up to 13.5 mm by Avila-Poveda & Baqueiro-Cárdenas (2006) and 15 mm by Stoner et al. (2012c). In our study, the mean shell length and lip thickness for adults involved in reproductive activity were 216 and 16 mm, respectively, supporting the suggestion that an increase from the current minimum lip thickness limit of 9.5 mm may further aid in the protection of adult queen conch and contribute to the recovery of depleted conch populations.

Essential in interpreting survey data on queen conch distribution and abundance is the consideration of depensatory mechanisms resulting in reduced per capita population growth rates and poor recovery of the stock. Depensation, or demographic Allee effects, potentially impacts queen conch populations through depressed reproductive output due to low encounter rates of adults (Stoner & Ray-Culp 2000), reduced larval or juvenile survival (Gascoigne & Lipcius 2004a), or delayed functional maturity in young adults (Gascoigne & Lipcius 2004b). Appeldoorn (1988b) initially suggested that queen conch may have a critical density for egg production, and Stoner & Ray-Culp (2000) provided evidence for demographic Allee effects in queen conch populations, reporting a complete absence of reproduction in population densities of less than 48 conch ha⁻¹. In Colombia, however, reproductive activity demonstrated by the presence of egg masses was reported in areas with population densities as low as 24 and 11 conch ha⁻¹ (Gómez-Campo et al. 2010). The scale over which these varied observations were recorded and subsequent interpretation of the spatial dispersion of queen conch may be critical to understanding

differences among study conclusions. Mating or spawning was associated with only 2.4% of the individual adult conch we located; however, the lowest mean density of adults at survey sites where reproductive activity occurred was 63.7 adults ha^{-1} . Except for 1 female laying eggs in areas open to fishing (overall adult density = 40.9 conch ha^{-1}), all reproductive activity in our study area occurred inside BIRNM boundaries (overall adult density = 86.2 conch ha^{-1}). The disparity in reproductive activity of adult queen conch may be linked to the overall density difference between the 2 management zones. Modeling studies have indicated that fishery exploitation strongly affects population persistence, particularly when multiple demographic Allee effects are present (Gascoigne & Lipcius 2004c), and our densities could represent potential reproductive threshold levels for each management area.

The potential movement of adults across the reserve boundary needs to be investigated further since models of marine reserve populations indicate that spillover of large adults can better sustain fishery yields, particularly for demersal species (Miethe et al. 2010). The presence of larger and older individuals, higher density of adults, and greater frequency of reproductive activity within the no-take reserve compared to the open fishing grounds implies that the spatial protection within BIRNM is effective and that its higher reproductive capacity is supporting queen conch stocks beyond the boundaries of the reserve (Sobel & Dahlgren 2004).

Comparisons of density estimates among studies are difficult due to inconsistencies in spatial and seasonal distribution patterns of queen conch, geographic variability, and differences in survey methods. The most commonly reported methods are belt transect surveys conducted by towing a diver from a boat (Stoner & Schwarte 1994, Stoner & Ray 1996, Stoner 2003, Stoner et al. 2012a), divers using scooters (Friedlander et al. 1994, Mateo et al. 1998), or paired divers swimming in parallel lines along a transect (Posada et al. 1999, Tewfik & Béné 2000, Béné & Tewfik 2003, Gordon 2010, Stoner et al. 2012a). Diver speeds are rarely reported, but they vary from 17 m min^{-1} (Stoner et al. 2012a) to 36 m min^{-1} (Friedlander et al. 1994). Field surveys employing these methods may overlook small individuals and result in underestimates of abundance because divers are moving rapidly over the substrate (Lincoln Smith 1988). Many of the previously mentioned surveys using transects only quantified adult conch (e.g. Friedlander et al. 1994, Stoner & Schwarte 1994, Stoner et al. 2012a,b, Cala et al. 2013) and therefore lack data on small

juveniles, an important component of the population. When conducting linear transect surveys, divers must also be meticulous in following an exact heading, traveling a straight line, and excluding conch that lie just outside the selected transect width. Radial surveys omit much of this sampling variability, are consistently reproducible, allow definitive recording of habitat types and depths, and provide an exact areal coverage for calculating densities (Bohnsack & Bannerot 1986), thereby reducing heterogeneity in population density estimates (Stoner & Ray-Culp 2000).

We were unable to directly compare habitat-specific conch densities across the duplicate survey locations because our characterization of the benthic community differed dramatically from the SEAMAP-C designation at each site. However, we were able to compare densities across general habitat categories using the overall means calculated from our study and the data available in the SEAMAP-C report (Gordon 2010). Similar to findings in other reports (Delgado et al. 1998, Mateo et al. 1998, Posada et al. 1999), queen conch densities in both studies were highest in seagrass. Queen conch remain buried in the sediment for much of their first year of life, emerging for short periods at night most likely to feed (Randall 1964, Sandt & Stoner 1993). In some areas, dense aggregations of newly emerged juveniles undergo mass migrations across seagrass meadows away from larval settlement areas. Movement rates of this potential density-dependent dispersal mechanism from recruitment centers have been reported (Stoner et al. 1988), but these movements are highly variable and in need of additional study. Predation pressure during this time is very high (Appeldoorn 1988c), and the structure of seagrass beds potentially decreases mortality risk (Ray & Stoner 1995). Large juveniles and adults typically exhibit an ontogenetic shift in habitat utilization and move from seagrass nursery habitat to algal plains or sand (Sandt & Stoner 1993, Doerr & Hill 2013). In our study area, however, conch either remained in seagrass habitats well into maturity or returned to them in association with seasonal reproductive migrations. This prolonged residency implies that seagrass may be providing an alternate ecological function for these conch, such as optimal forage, or alternatively a reproductive benefit since adults in our surveys mated and spawned primarily in seagrass habitats. Adult queen conch are historically reported to mate and spawn in clean sand with low organic content (Randall 1964, Brownell & Stevely 1981, Glazer & Kidney 2004), and it should be noted that sand was

the dominant substrate underlying the seagrass habitats where reproductive activity was observed in this study.

Despite the difficulties in conducting legitimate cross-study density comparisons, the overall density of queen conch on the northeastern shelf of St. Croix appears to be stable and potentially increasing. We estimated an overall density of 302.1 conch ha⁻¹ (233.5 juveniles ha⁻¹ and 68.5 adults ha⁻¹) in our study. Pittman et al. (2008) completed biannual randomized belt transect surveys of reef fish and macro-invertebrates covering 6.24 ha across multiple habitat types in adjacent areas on the northeastern coast of St. Croix from 2004 to 2006 and reported an overall density of approximately 118.0 conch ha⁻¹ (85.3 juveniles ha⁻¹ and 32.7 adults ha⁻¹). Small or inconspicuous queen conch may be underrepresented in their density estimates, however, since queen conch were not the primary target of the surveys. In the 5 transect surveys conducted within our study area in 2009, the SEAMAP-C surveys (Gordon 2010) estimated an overall density of 264.5 conch ha⁻¹ (170.0 juveniles ha⁻¹ and 94.5 adults ha⁻¹). However, it should be noted that 3 of the 5 permanent SEAMAP-C transect sites were located south of Buck Island primarily in moderate to dense seagrass habitats representative of juvenile queen conch nursery areas. The mean densities from our radial surveys conducted at the same 5 transect sites are comparable to the reported SEAMAP-C densities (338.9 conch ha⁻¹ overall, 279.8 juveniles ha⁻¹, and 59.1 adults ha⁻¹) and likely demonstrate the patchiness of the queen conch population distribution in the area rather than temporal changes in density.

Accurate and complete data collection to support management decisions is essential if queen conch stocks are to recover fully and remain an important cultural and economic resource throughout the region. In particular, the potential existence of Allee effects within a queen conch population on a local or regional level should provide strong incentive to continue and expand fishery-independent surveys of conch densities. Understanding spatial distribution and dispersion is critical to effective management. However, spatial context is generally lacking in fishery-dependent datasets that have been the basis for traditional stock assessment models, which contributes to increased uncertainty and, potentially, to mismanagement and overexploitation of stocks (Stergiou 2002). Fishery-independent monitoring surveys, particularly when used to evaluate the efficacy of marine reserve areas and conditions during closed seasons, are an effective way to support successful management strategies. However, employing consis-

tent sampling approaches and evaluating synergistic effects of multiple variables are challenging aspects of these types of studies. The high densities of small and large juvenile queen conch documented in our study indicate that local recruitment has been persistent and successful. The densities of juvenile and adult conch reported in this study suggest that at least 3 events are occurring within the area: (1) larval recruitment, larval retention, or both are high; (2) juvenile queen conch are reaching maturity successfully and are supplementing the reproductive population; and (3) BIRNM is functioning effectively as a marine protected area for all life stages of queen conch.

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